

# Splendid Innovation: The Extinct South American Native Ungulates

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## Keywords

Astrapotheria, evolution, Litopterna, Meridiungulata, Notoungulata, paleoecology

## Abstract

A remarkable diversity of plant-eating mammals known as South American native ungulates (SANUs) flourished in South America for most of the Cenozoic. Although some of these species likely filled ecological niches similar to those of modern hoofed mammals, others differed substantially from extant artiodactyls and perissodactyls in their skull and limb anatomy and probably also in their ecology. Notoungulates and litopterns were the longest-lived and most diverse SANU clades and survived into the Quaternary; astrapotheres went extinct in the late Miocene, whereas other SANU groups were restricted to the Paleogene. Neogene notoungulates were quite specialized in craniodental structure, but many were rather unspecialized postcranially; in contrast, litopterns evolved limb specializations early in their history while maintaining more conservative dentitions. In this article, we review the current understanding of SANU evolutionary relationships and paleoecology, provide an updated compilation of genus temporal ranges, and discuss possible directions for future research.

- South American native ungulates (SANUs) were a diverse, long-lived, and independent radiation of mammals into varied terrestrial plant-eater niches.

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- We review origins, evolution, and paleoecology of the major SANU clades: Notoungulata, Litopterna, Astrapotheria, Xenungulata, and Pyrotheria.
- At their peak, during the Eocene and Oligocene, more than 40 genera of native ungulates inhabited South America at any one time.
- SANUs ranged from <1 kg to several tons and evolved many combinations of diet and locomotor adaptations not seen in living ungulates.

## INTRODUCTION

South American native ungulates (SANUs) were once ubiquitous inhabitants of this southern continent and filled a wide variety of ecological niches. The hundreds of extinct species that have been discovered thus far pertain to at least five orders and some two dozen families and span a remarkable range of shapes and sizes. During most of the Cenozoic, SANUs and xenarthrans, the latter represented today by some 30 species of sloths, armadillos, and anteaters, were the predominant medium- to large-sized plant-eaters in South America. Humans undoubtedly interacted with SANUs near the end of the Cenozoic and probably had a contributing if not major role in their extinction (Cione et al. 2003, Barnosky & Lindsey 2010). However, SANUs were already in decline long before humans arrived in South America. By the Pleistocene, they were represented by only a handful of species, although these final representatives were so unlike modern mammals that their fossil remains helped fuel Darwin's belief in the mutability of species (Cain 1984, Fernicola et al. 2009, Brinkman 2010).

What is it about SANUs that makes them fascinating? Although some SANUs evolved features similar to those of extant ungulates, others developed novel anatomical solutions to universal ecological and environmental challenges. Analyzing these instances of convergent evolution and morphological innovation can lead to new insights into how mammals respond to selective pressures. Modern ungulates provide just a few examples of how mammals can occupy medium- and large-bodied terrestrial herbivore niches; the evolutionary experiment of SANUs is rife with others. On a broader scale, because South America's Cenozoic mammals evolved in relative isolation (Simpson 1980), they are like a replicate experiment in biological evolution and can be used to test patterns of diversity and adaptation developed on other continents. SANUs were diverse and abundant during most of the Cenozoic, and an accurate appreciation of their roles in ancient ecosystems is necessary for broader investigations of how mammal communities have responded to tectonic events and trends in global climate (e.g., Pascual & Odreman Rivas 1973, Woodburne et al. 2014).

Not all SANUs were ungulates in the strict sense of the word (i.e., hoofed mammals). Many litopterns had hooves remarkably similar to those of living horses, rhinos, or pigs, but some notoungulates had claws (e.g., *Homalodotherium*), and others had something in between a claw and a hoof (e.g., *Notostylops*; Lorente et al. 2019). Some SANUs supported themselves with only one or two digits on each foot like a horse or a cow, whereas others walked on four or five digits like most other mammals. Many SANUs were of medium to large size (tens to hundreds of kilograms), but many others were small (<10 kg) and some were smaller than any ungulate alive today (around 0.5 kg). SANUs spanned a wide range of forms: Some resembled living antelopes (Bovidae), camels (Camelidae), or horses (Equidae); others were closer to rhinos (Rhinocerotidae), hippos (Hippopotamidae), or even elephants (Proboscidea), and many resembled large rodents (Rodentia), rabbits (Lagomorpha), or even plant-eating marsupials (Metatheria: Diprotodontia) (**Figure 1**).

### Ungulate:

a descriptive (rather than taxonomic) term for plant-eating mammals in which the ends of the digits are modified into hooves

**Xenarthra:** one of four primary groups of placental mammals; includes sloths, armadillos, anteaters, and relatives





**Figure 1**

Life reconstructions of South American native ungulates (SANUs), labeled by family, with higher classification in colored rectangles. (a) Macraucheniidae: *Theosodon lallemanti* (125–170 kg). (b) Protheroetheriidae: *Neobrachytherium ullumense* (25–45 kg). (c) Leontiniidae: *Anayatherium fortis* (280–370 kg). (d) Interatheriidae: *Santiagorothia chiliensis* (5–7 kg). (e) Toxodontidae: *Toxodon platensis* (1,000–1,200 kg). (f) Mesotheriidae: *Typotheriopsis chasicensis* (22–33 kg). (g) Astrapotheriidae: *Granastrapotherium snorki* (1,800–2,500 kg). (h) Pyrotheriidae: *Pyrotherium romeroi* (3,000–3,500 kg). Reconstructions (by Velizar Simeonovski) and body mass estimates from Croft (2016).

**Table 1** Summary information for the seven South American native ungulate (SANU) groups discussed in the text

Order	Description
Astrapotheria (19 genera, 2 families)	Generally large to very large (100 to 1,000+ kg), with canine tusks and a large gap between them and the low-crowned, rhino-like cheek teeth. Some had retracted nasal bones, suggesting a proboscis. May have preferred moist, lowland habitats.
Didolodontidae (13 genera)	Small (<~10 kg), bunodont, and perhaps frugivorous. Known only from dental remains.
Kollpaniinae (6 genera)	Small (<1 kg) condylarths with relatively unspecialized teeth compared to other plant-eaters. Known only from dental remains.
Litopterna (67 genera, 9 families)	Small to very large (1–1,000 kg); most similar SANUs to extant ungulates in overall form. Bunodont to lophodont dentitions, low-crowned to slightly hypsodont; cursorial postcranial specializations present early in the group's history. Proterotheriids were generally 10s of kg, had one functional toe on each foot, and evolved tusk-like incisors separated from the cheek teeth by a large gap. Macraucheniiids were generally ~100–1,000 kg, had three functional toes on each foot, and never evolved large gaps in their dentition or enlarged incisors or canines. In Pleistocene <i>Macrauchenia</i> , the external bony nostrils were positioned on the dorsal aspect of the skull between the orbits. Some Paleogene litoptern families have been referred to a separate order, Notopterna.
Notoungulata (~150 genera, ~14 families, 2 suborders)	Small to very large (1–1,000 kg); greatest diversity in size and form among SANUs. Members of suborder Toxodontia generally 10s of kg to 1,000 kg, mostly with robust, unspecialized limbs. The family Homalodotheriidae included relatively long-limbed, clawed species, and a few toxodontids may have had a rhino-like horn. Members of suborder Typotheria generally ~1–10s of kg, some with cursorial specializations, otherwise unspecialized or adapted for digging. Predominantly hypsodont to hypselodont (ever-growing) dentitions from Oligocene onward. Some typotheres evolved rodent-like incisors and muscles of mastication.
Pyrotheria (~7 genera, 1 family)	Generally large to very large (100s to 1,000+ kg), with incisor tusks, distinctive bilophodont teeth, and retracted nasal bones, suggesting a proboscis. Genera other than <i>Pyrotherium</i> known only from partial dentitions; very little is known of the skeleton of <i>Pyrotherium</i> .
Xenungulata (4 genera, 2 families)	Large (10s to 100s of kg) with bilophodont teeth similar to pyrotheres. Skeletal remains from one species are known but presently undescribed. Skull (other than mandible/maxilla) basically unknown.

SANUs are divided today into five major groups (Notoungulata, Litopterna, Astrapotheria, Pyrotheria, and Xenungulata) and several minor groups whose phylogenetic relationships are not completely resolved (e.g., Didolodontidae, Kollpaniinae) (Table 1). Together, these major groups include some 50 families and well over 250 genera (Figure 2). In this review, we focus on two areas in which knowledge of South America's strange hoofed mammals has undergone major developments in recent decades: phylogenetic relationships and paleoecology.

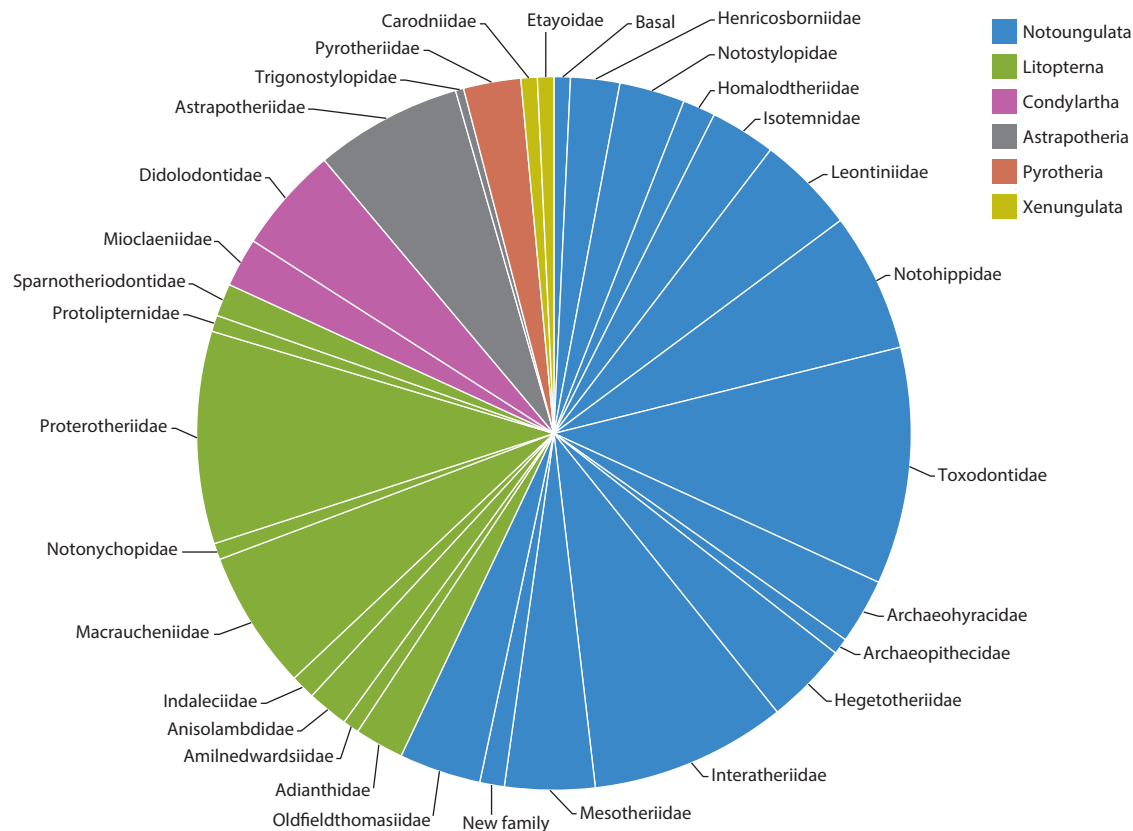
## PHYLOGENETIC RELATIONSHIPS

### Broader Relationships

Whether all SANUs constitute a single clade that excludes non-South American taxa (i.e., Meridiungulata of McKenna 1975) remains a fundamental question of SANU evolutionary relationships, yet no cladistic analysis has explicitly aimed to test this hypothesis. Two studies based on collagen protein data from Pleistocene SANUs have provided support for a partial Meridiungulata clade by finding a sister-group relationship between notoungulates (*Toxodon platensis*) and litopterns (*Macrauchenia patachonica*) and a closer relationship between them and perissodactyls than any other placental mammal group (Buckley 2015, Welker et al. 2015) (Figure 3a,b). The grouping of SANUs and perissodactyls (collectively termed Panperissodactyla) suggests that at

**Clade:** a group that includes an ancestor and all of its descendants (as opposed to just some of its descendants); also known as a monophyletic or natural group





**Figure 2**

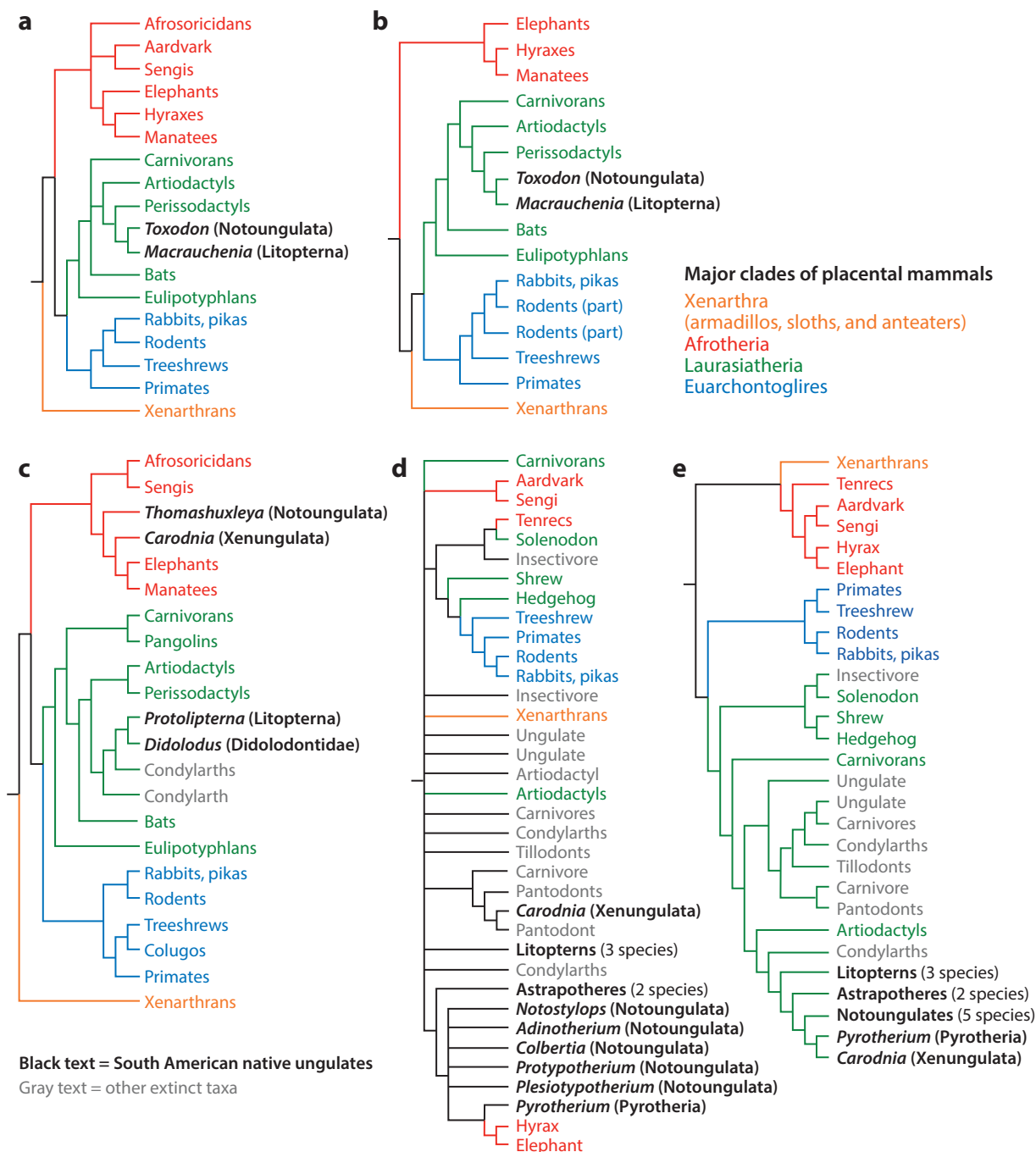
South American native ungulate (SANU) diversity expressed as a percentage of genera of each family, with major SANU groups coded by color.

least these SANUs are members of Laurasiatheria, in agreement with inferences based on paleogeographic reconstructions of South America. A subsequent analysis of mitochondrial DNA from *Macrauchenia* corroborated litopterns as members of Laurasiatheria, most closely related to perissodactyls among extant mammals (Westbury et al. 2017). SANU groups other than notoungulates and litopterns predate the late Miocene (**Figure 4**), which makes obtaining similar molecular data for them particularly challenging.

Morphological and combined morphological-molecular analyses have yet to provide conclusive support for Meridiungulata monophyly. The analysis of O'Leary et al. (2013) included four SANUs among its 86 taxa: a notoungulate (middle Eocene *Thomasbuxleya externa*), a xenungulate (early Eocene *Carodnia vieirai*), a litoptern (early Eocene *Protolipterna ellipsodontoides*), and a didolodontid (middle Eocene *Didolodus multispis*). In the best-supported tree that combined morphological and molecular evidence, SANUs formed two groups rather than a single Meridiungulata; the litoptern and didolodontid were recovered within Laurasiatheria, equally closely related to perissodactyls and artiodactyls (as part of a clade including non-South American so-called condylarths), whereas the xenungulate and notoungulate were found to be afrotherians, positioned as successive outgroups to Tethytheria (elephants and manatees) (**Figure 3c**). Afrotherian affinities for some SANUs are not a novel hypothesis (Agnolín & Chimento 2011),

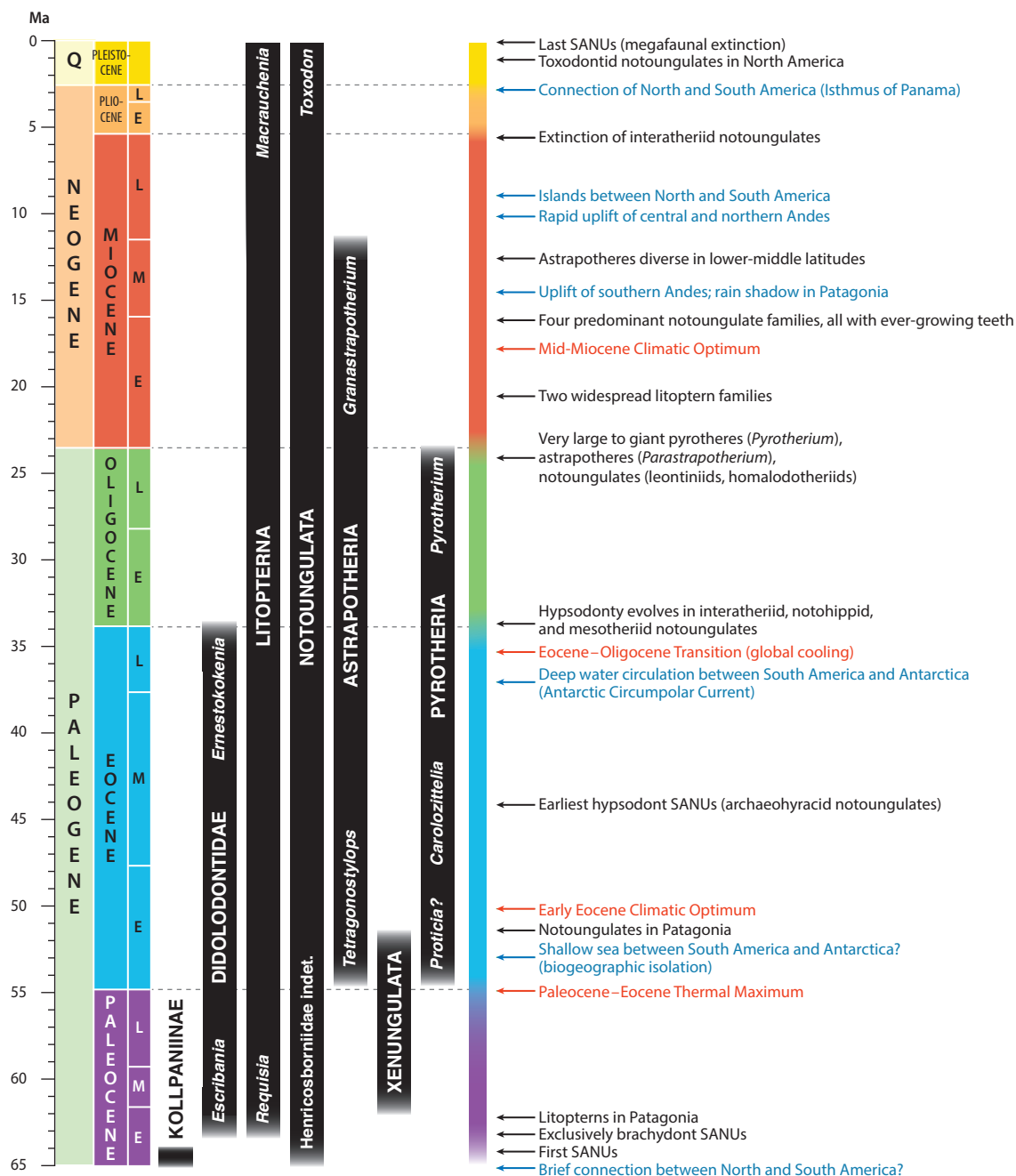
**Laurasiatheria:** One of four primary groups of placental mammals; includes mammals that probably evolved in the Northern Hemisphere on the supercontinent Laurasia, such as carnivorans, pangolins, bats, ungulates, shrews, and hedgehogs

**Condylarth:** member of an artificial (non-monophyletic) and now informal grouping of extinct mammals thought to be closely related to modern ungulates



**Figure 3**

Cladograms illustrating possible phylogenetic relationships of South American native ungulates (SANUs) among placental mammals. Cladograms adapted from (a) Welker et al. (2015); (b) Buckley (2015); (c) O'Leary et al. (2013); (d) de Muizon et al. (2015; unconstrained consensus cladogram); (e) de Muizon et al. (2015; one of the most parsimonious trees obtained using a molecular scaffold for relationships of extant placentals).



**Figure 4**

Cenozoic geologic timescale with temporal ranges of South American native ungulate (SANU) groups (see also **Table 2**); selected noteworthy events in SANU evolution (*black arrows* and text), global climate (*red arrows* and text), and tectonics (*blue arrows* and text) are also included. Earliest- and/or latest-occurring genera are noted for most taxa.



**Afrotheria:** one of four primary groups of placental mammals; includes mammals that probably evolved in Africa, such as elephants, manatees, hyraxes, aardvarks, sengis, tenrecs, and golden moles

**Monophyletic:** a group that includes a common ancestor and all of its descendants

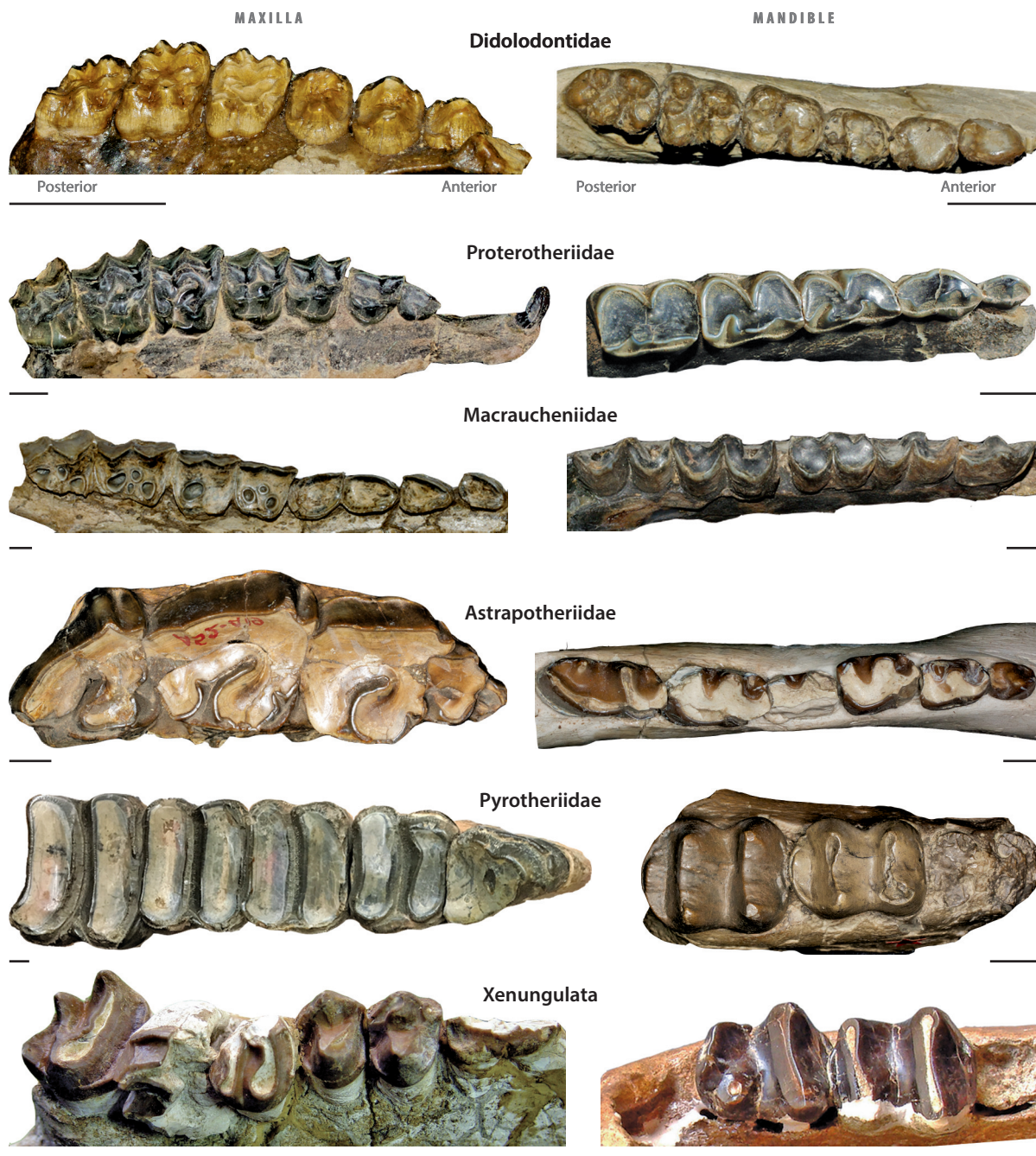
**Bunodont:** having teeth with low, rounded cusps

but it is unlikely considering (a) the molecular evidence noted above, (b) some afrotherian features allegedly present in notoungulates have been incorrectly interpreted or refuted (Billet & Martin 2011, Kramarz & Bond 2014a; see also Gelfo & Lorente 2012), and (c) the improbable paleogeographic scenario that it implies considering the breakup of Gondwana and the tectonic evolution of South America during the Cenozoic (Pascual et al. 1996). Indeed, when Carrillo & Asher (2017) modified the codings of *Thomasbuxleya* in the O’Leary et al. (2013) matrix, incorporated SANU molecular data, and constrained Notoungulata and Litopterna to be monophyletic, the optimal Bayesian tree recovered both clades within Laurasiatheria, most closely related to perissodactyls.

Twelve SANUs (five notoungulates, three litopterns, two astrapotheres, one pyrothere, and one xenungulate) were among the 72 extinct and extant eutherians analyzed by de Muizon et al. (2015), who were interested in resolving the phylogenetic relationships of the pantodont *Alcidedorbignya inopinata* (early Paleocene of Bolivia). The strict consensus tree from their unconstrained analysis resulted in a large polytomy (16 branches) that failed to recognize Meridiungulata or even most commonly accepted supraordinal groups (Figure 3d). Instead, SANUs were distributed among three clades: litopterns (as a separate branch), the xenungulate (as a member of Pantodonta), and a clade including astrapotheres, notoungulates, pyrotheres, and paenungulates (i.e., elephants and hyraxes). When the topology was constrained to include the four main clades of extant mammals that have been recovered by molecular analyses, a monophyletic Meridiungulata was recovered, nested within Laurasiatheria and sister to a clade of North American condylarths (Figure 3e). As highlighted by de Muizon et al. (2015), this tree is rife with independent evolution of similar features in distinct groups and very sensitive to the inclusion or exclusion of taxa. Moreover, no representative of Perissodactyla was included in the analysis, so the Panperissodactyla hypothesis was not tested.

Key to understanding broader relationships of SANUs is resolving the relationships of South America’s condylarths, which include Kollpaniinae and Didolodontidae. Kollpaniines include several taxa from the early Paleocene of Bolivia (Figure 4) and an isolated record from the Eocene of Patagonia (Gelfo 2004) that awaits further confirmation. Kollpaniines may be closely related to North American Mioclaenidae (de Muizon & Cifelli 2000, de Muizon et al. 2015), but no consensus about Mioclaenidae taxonomy has been achieved; some studies have argued that most mioclaenids should be included within North American Hyopsodontidae, leaving the Kollpaniinae as an independent monophyletic group restricted to South America (Zack et al. 2005, Williamson & Carr 2007).

Didolodontids are small- to medium-sized bunodont ungulates mainly known from Paleocene and Eocene sites in Argentina (Figure 4). They show some evolutionary novelties with respect to kollpaniines, such as more crushing tooth cusps and a true hypocone in the upper molars (Gelfo 2006, 2007, 2010) (Figure 5). In the phylogenetic analysis of de Muizon & Cifelli (2000), didolodontids, kollpaniines, and North American mioclaenids were positioned as successive outgroups to Litopterna (although not as distinct branches). This clade, which they termed Panameriungulata, suggests a North American origin for litopterns. O’Leary et al. (2013) did not include mioclaenids in their analysis but, as noted previously, did find a sister-group relationship between didolodontids and litopterns, with North American condylarths as more basal representatives of that clade (Figure 3c). A close relationship between North American mioclaenids and SANUs was dismissed by Williamson & Carr (2007) and was not tested by de Muizon et al. (2015). Even if kollpaniines do share a common origin with North American mioclaenids, the evolutionary linkages between these groups and perissodactyls remain to be determined. Although no associated postcranial remains of kollpaniines or didolodontids have been found, possible associations of disarticulated bones with isolated teeth have been inferred using regression equation models (Cifelli 1983a, Bergqvist 1996, de Muizon et al. 1998). These proposed associations have been strongly



All scale bars = 1 cm

(Caption appears on following page)

Figure 5 (Figure appears on preceding page)

Representative partial upper (left column) and lower (right column) teeth of South American native ungulates (SANUs); anterior toward right in all images, with tooth positions numbered sequentially from the front. Didolodontidae: *Didolodus multicuspis* (upper left P2–M3, shown as right, MACN A 10690; lower right p2–m3, MACN A 10689). Proterotheriidae (Litopterna): *Diadiaphorus majusculus* (upper right C–M3, MLP 12–304; lower left p1–m1, MLP 12–351). Macraucheniiidae (Litopterna): *Promacrauchenia antiqua* (upper left C–M3 shown as right, FMNH PM 14517; lower left p3–m3, MACN A 7986). Astrapotheriidae (Astrapotheria): *Astrapothericulus iberingi*; (upper left P3–M3 shown as right, MACN A 52–419), *Astraponotus* sp. (lower right p2–m3; MLP 82–V-7-2). Pyrotheriidae (Pyrotheria): *Pyrotherium romeroi* (upper right P3–M3, FMNH PM 13515), *Griphodon peruvianus* (left lower p4–m1, cast of AMNH 17724). Xenungulata: *Carodnia vieirai* (upper left P2–M3, shown as right, DGM 333–M), *Carodnia inexpectans* (lower right m2–3, MUSM-2025). Abbreviations: AMNH, American Museum of Natural History, New York, USA; c/C, canine; DGM, Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; FMNH, The Field Museum, Chicago, USA; m/M, molar; MACN, Museo Argentina; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor San Marcos, Lima, Peru; p/P, premolar.

criticized (Wyss et al. 1994, Soria 2001, Gelfo & Lorente 2010, Lorente 2015), and very probably only those made for Kollpaniinae and Protolipternidae are valid.

Pyrotheres and xenungulates have been proposed to be closely related to North American uin-tatheres (Dinocerata) (Lucas 1986). This proposal has yet to be thoroughly tested, but at present, there is no strong evidence that resemblances between these two groups and uin-tatheres represent synapomorphies (Cifelli 1993, Shockey & Anaya 2004, Gelfo et al. 2008; see also the sections titled Pyrotheria and Xenungulata below).

## Notoungulata

Since the cladistic analysis of Cifelli (1993), modern understanding of notoungulate relationships has recognized two main clades, Typotheria and Toxodontia, and two early-diverging families, Notostylopidae and Henricosborniidae. In ensuing years, the only study to comprehensively tackle notoungulate intraordinal relationships has been Billet (2011), who coded 50 notoungulates and eight other taxa for 133 craniodental characters. The strict consensus tree from this study is broadly congruent with the family-level analysis of Cifelli (1993), with the notable exception of *Pyrotherium* being positioned within Notoungulata (discussed below). Billet (2011), like Cifelli (1993), found several traditionally recognized notoungulate families to be nonmonophyletic, including henricosborniids (stem notoungulates), isotemnids (stem toxodontians), no-tohippids (stem toxodontids), oldfieldthomasiids (stem typotherians), and archaeohyracids. However, some groups (e.g., Henricosborniidae, Notostylopidae) were represented by only a few or a single taxon, leaving open the possibility that adding other representatives could affect the resulting topology.

## Litopterna

Despite the great diversity and rich fossil record of this group, much work remains to be done regarding its phylogenetic relationships. Most taxonomic arrangements have not been tested by broad cladistic analyses, so suprafamilial classification schemes, such as those proposed by Cifelli (1983b, 1993) and McKenna & Bell (1997), should be considered provisional.

Cifelli (1983b) divided litopterns into two main groups: Macraucheniiidae and related forms and species related to Proterotheriidae. A third group, Protolipternidae, was erected to encompass two species (*Protolipterna ellipsodontoides* and *Miguelsoria parayirunhor*) with derived ankle (tarsal) morphologies similar to litopterns but bunodont dentitions like didolodontids (Cifelli 1983b, 1993). Indeed, one of these species (*M. parayirunhor*) was originally described as a didolodontid before associations between dental and postcranial remains were inferred (de Paula Couto 1952).



Soria (2001, p. 156) hypothesized that all didolodontids probably had a litoptern-like tarsus, and this proposal has yet to be refuted. This would make Protolipternidae a junior synonym of Didolodontidae and didolodontids bunodont litopterns (cf. Gelfo et al. 2016, table 1).

Although details of cladistic analyses using postcranial characters have yet to be published (e.g., Bergqvist 2005), it is clear that early selective pressures triggered important evolutionary novelties in the litoptern locomotor system. This contrasts with notoungulates, in which postcranial features are more conservative. Litopterna has not been recovered as a monophyletic group in studies that have not included postcranial data; for example, in the unconstrained craniodental analysis of Billet et al. (2015), generally recognized litopterns were part of a polytomy with *Didolodus* and several North American condylarths (Billet et al. 2015, figure 14). However, testing the monophyly of Litopterna was not a goal of that study. Resolving intraordinal relationships of litopterns will undoubtedly require an analysis with a broad combination of postcranial and craniodental data sets.

One long-standing issue in litoptern systematics is whether *Indalecia grandensis* from the middle Eocene Lumbrera Formation of northwest Argentina (see del Papa et al. 2010) falls within or outside Litopterna. The species was originally identified as an adianthid litoptern (Bond & Vucetich 1983) and was later placed in a distinct order, Notopterna, along with several other taxa (Soria 1989). A preliminary study of the auditory region of *Indalecia* has supported a divergence prior to the common ancestor of litopterns (García-López & Babot 2014), a position potentially analogous with that of the purported astrapothere *Eoastrapostylops* (Kramarz et al. 2017; discussed in the section titled Astrapotheria below). If correct, then other taxa thought to be closely related to *Indalecia*, such as *Adiantoides* from the Eocene of Divisadero Largo and Cañadón Vaca, Argentina (Cifelli & Soria 1983, López 2010), may also pertain to a clade separate from Litopterna. The cladistic analysis of Bonaparte & Morales (1997) found that *Indalecia*, as well as other taxa originally referred to Notopterna (*Notomyschops*, *Requisia*), represent basal litoptern lineages rather than a distinct, monophyletic group. Therefore, at present, the status of Notopterna as a separate SANU group is dubious.

The Sparnotheriodontidae (Litopterna) seem to have been one of only two SANU groups (along with Astrapotheria) to reach the Antarctic continent during the early Eocene (Bond et al. 2011, Gelfo 2016). This family was originally considered Notoungulata *incertae sedis* (Soria 1980b) and later referred to the Litopterna (Soria 1980a, 2001), closely related to Anisolambdidae (Soria 2001). Based on potentially associated dental and postcranial remains, sparnotheriodontids were considered to be condylarths (e.g., Cifelli 1983b). However, as noted previously, such associations have been criticized and regarded as unreliable (Wyss et al. 1994, Soria 2001, Gelfo & Lorente 2012, Lorente 2015, Gelfo 2016). Based on available information, referral of Sparnotheriodontidae to Litopterna seems to be the simplest arrangement (Soria 2001, Bond et al. 2006).

## Astrapotheria

Astrapotheres were traditionally divided into two (or more) subfamilies, Trigonostylopidae and Astrapotheriidae, but only the latter appears to be a natural group (Kramarz & Bond 2011). Cifelli (1993, p. 201) “arbitrarily defined” Astrapotheriidae as the monophyletic group including late Eocene *Astraponotus* and later astrapotheres (*Astrapotherium*, *Parastrapotherium*, and *Astrapothericulus* in his analysis). Since then, five new astrapothere genera have been named (including *Antarctodon*, an Antarctic endemic) as well as additional species of *Xenastrapotherium* (Johnson & Madden 1997, Bond et al. 2006, Vallejo-Pareja et al. 2015). As a result, the vast majority of astrapotheres are included in Astrapotheriidae, and most recent phylogenetic analyses have focused on relationships within this family and the subfamily Uruguaytheriinae (e.g., Carrillo et al. 2018). Uruguaytheriinae includes all astrapotheres presently known from tropical latitudes,

### Bilophodont:

having teeth with two transverse crests

**Enamel:** the hardest and most mineralized tissue in a tooth; usually forms cusps, crests, or lophs for breaking down food

some of which are also the geologically youngest representatives of the order (Goillot et al. 2011, Croft et al. 2016).

*Eoastrapostylops riolorensis*, from the Paleocene or early Eocene Río Loro Formation of northwest Argentina, was originally described as a primitive astrapothere (Soria & Powell 1981), and since then, it has generally been considered to be the basalmost member of the order. Additional preparation and restudy of the holotype skull have cast doubt on this referral. Kramarz et al. (2017) tested the phylogenetic position of *Eoastrapostylops* using modified versions of the matrices of de Muizon et al. (2015) and Billet et al. (2015) and a third matrix that combined the two. *Eoastrapostylops* occupied distinct positions in all analyses, suggesting that it may not pertain to any SANU order. In the two analyses in which a monophyletic Astrapotheria (represented by *Astrapotherium* and *Trigonostylops*) was recovered, *Eoastrapostylops* was basal to a group that included notoungulates, xenungulates, and pyrotheres in addition to astrapotheres.

## Pyrotheria

A major impediment to clarifying pyrothere relationships is that virtually all members of the group are known from relatively incomplete dental remains (see Kramarz & Bond 2014b). The sole exception is late Oligocene *Pyrotherium*, the geologically youngest pyrothere; a specimen collected more than a century ago is the only skull known for the order. Many other teeth and partial jaws of *Pyrotherium* have been collected from sites throughout much of South America, as have some postcranial elements (Shockey & Anaya 2004).

Patterson (1977) noted many resemblances between the auditory regions of *Pyrotherium* and notoungulates, and Billet (2010) breathed new life into Patterson's idea that pyrotheres were notoungulates by noting additional resemblances between the anterior dentitions of *Pyrotherium* and the early-diverging notoungulate *Notostylops*. Billet's (2010) phylogenetic analysis included 141 characters and 64 taxa, mainly notoungulates (50 genera) and pyrotheres (7 genera), but it did not include any xenungulates, the only SANUs besides pyrotheres with bilophodont teeth (**Figure 5**). In the strict consensus tree, pyrotheres other than *Proticia* formed a clade separate from notoungulates; removing *Proticia* (a questionable pyrothere; discussed further later in this section) resulted in pyrotheres being nested within a monophyletic Notoungulata, as the sister-group of *Notostylops*, a position driven by inner skull characters to the detriment of dental characters. In the constrained analysis of de Muizon et al. (2015), which used characters of Billet (2010) but incorporated xenungulates (among other taxa), bilophodont SANUs were recovered as a natural group, sister to notoungulates (**Figure 3e**). Although the inclusion of pyrotheres within Notoungulata based on cranial similarities has yet to gain wide acceptance, this intriguing hypothesis has generated new interest in a close relationship between them and has revitalized discussion of the evolutionary value of characters from different parts of the body.

Whether *Proticia venezuelensis* is a pyrothere remains an open question. The holotype jaw was described by Patterson (1977) as coming from the Paleocene–Eocene Trujillo Formation, but it may instead derive from the Miocene Castillo Formation and represent a manatee (sirenian) (Sánchez-Villagra et al. 2000). A rare earth element or petrographic analysis could prove useful for determining the stratigraphic provenance and age of the only known specimen. Another strategy could be to examine the microscopic structure of the specimen's enamel. As demonstrated by von Koenigswald et al. (2015), pyrothere teeth have distinctive keyhole enamel prisms, which have otherwise been identified only in elephants (proboscideans), hominids, and a group of Paleogene mammals known as taeniodonts. If *Proticia* is a pyrothere, its teeth should have similar enamel prisms.

The absence of keyhole enamel prisms in early-diverging notoungulates such as *Henricosbornia* and *Notostylops* (Maas 1997) would seem to favor the interpretation that dental similarities between *Pyrotherium* and *Notostylops* were acquired convergently. However, more complete craniodental remains of more basal pyrotheres, such as *Propyrotherium* and *Colombitherium*, are needed to more confidently test this hypothesis. Postcranial remains from Eocene pyrotheres might also prove useful for clarifying whether pyrotheres diverged from within Notoungulata or represent its sister-group.

## Xenungulata

Xenungulates have been found at Paleocene and early Eocene sites throughout South America (Gelfo et al. 2008, Antoine et al. 2015). As noted previously, they have been thought to be closely related to pyrotheres based on the shared presence of bilophodont first and second molars (Figure 5), but this condition could have evolved independently in the two groups, as it has in many other groups of mammals (von Koenigswald 2018). This inference is supported by the enamel microstructure of the xenungulate *Carodnia*, which lacks the keyhole prisms characteristic of pyrotheres (von Koenigswald et al. 2015, Bergqvist & von Koenigswald 2017), as well as the presence of cusped (rather than lophed) talonids in the xenungulate family Etayoidae, among other details of the dentition (Cifelli 1993, Gelfo et al. 2008).

## PALEOECOLOGY

A major challenge in reconstructing SANU paleobiology is the lack of living members of any SANU clade. Even if all major SANU groups turn out to be stem perissodactyls, as seems to be the case for litopterns and notoungulates, modern horses, rhinos, and tapirs are not close anatomical analogs for most SANUs. Even extant ungulates in the broad sense (i.e., artiodactyls, perissodactyls, hyraxes, and proboscideans) fail to circumscribe the anatomical variation seen in the main SANU groups. As a result, many paleoecological studies of SANUs have relied on wide comparative data sets of extant mammals to adequately span morphologies and ecologies. Taxon-independent methods (see Green & Croft 2018, Higgins 2018) have also proven useful for reconstructing SANU paleoecology and, in some cases, provided unexpected results.

## Body Mass

Body mass is one of the most common paleoecological parameters inferred for extinct mammals (see Hopkins 2018 for a recent review). Many body mass estimates have been published for SANUs, but the accuracy of these estimations is difficult to gauge given the lack of living representatives or close modern analogs. Damuth (1990) provided an excellent review of the difficulties in estimating body mass in extinct ungulates with no close living relatives and advocated using head-body length, when available. Head-body length has an obvious (and high) correlation with body mass and can help highlight biases that arise when using a particular anatomical feature to estimate mass in extinct species. For example, Cassini et al. (2012) calculated the body mass of the early Miocene toxodontid *Nesodon* at 500–800 kg based on craniodental measurements. Using the nonselenodont head-body length equation of Damuth (1990, table 12.4) and a head-body length estimate of 1.75 m for *Nesodon* (Scott 1912, pl. 12), its mass is estimated at 247 kg, less than half that calculated by Cassini et al. (2012). In contrast, the body mass estimate of Cassini et al. (2012) for the macraucheniid litoptern *Theosodon* (120–160 kg) is very close to the range of 125–170 kg published by Croft (2016) using several head-body length regression equations (see



McGrath et al. 2018). The concordance of these ranges, which are based on very different models, engenders greater confidence in their accuracy.

Why do craniodental body mass estimates appear to be inaccurate for toxodontid notoungulates but accurate for macraucheniid litopterns? The likely explanation is that toxodontids like *Nesodon* were relatively large-headed ungulates with ever-growing premolars and molars that are not closely similar to any ungulate alive today. Therefore, using ungulate craniodental variables to estimate body mass results in overestimates. *Theosodon*, however, was a medium-sized litoptern with dental and cranial proportions within the range of modern artiodactyls and perissodactyls. As a result, craniodental variables work well for estimating its mass. Similar issues can plague body mass estimates based on limb bone dimensions because most SANUs (particularly notoungulates) have short, stocky limbs compared to most extant ungulates (see later in this section). For example, limb bone-based body mass estimates for *Nesodon* calculated by Elissamburu (2012, table 2) range from 106.7 kg (humerus length) to 2,073.8 kg (humerus circumference). However, body mass estimates based on the astragalus are close to those calculated using head-body length (Carrillo & Asher 2017). Sometimes, correction factors can be employed to increase confidence in predictions (e.g., Scarano et al. 2011).

Kollpaniids were small SANUs (<5 kg) (Gelfo et al. 2016), commensurate with their Paleocene fossil record, but are only known from dental remains (as noted previously). The only published mass estimate is 250–500 g for *Molinodus suarezi* (Croft 2016). Didolodontids clearly spanned a larger range of sizes than kollpaniids, but no body mass estimates have been published for the group. Based on lower molar row length (Figure 5), *Didolodus multicuspis* had a body mass of ~10 kg (using the nonselenodont equation of Damuth 1990).

Early-diverging notoungulates (henricosborniids, notostylopids) from the Paleocene and Eocene were small to medium in size. Henricosborniids are mainly known from teeth and dentitions, but two species from northwest Argentina, *Simpsonotus praecursor* (Figure 5) and *Simpsonotus major*, are known from skulls that measure ~6.7 and 11.0 cm, respectively (Pascual et al. 1978). Assuming a head-body length of 4.5–5 times skull length (a typical ratio for small notoungulates; D.A. Croft, unpublished data), *S. praecursor* had a body mass of ~1 kg and *S. major* had a body mass of 3–4.5 kg. The notostyloid *Notostylops murinus*, the most completely known notostyloid, likely had a body mass between 5 and 13 kg based on head-body length and astragalus size (Croft 2016, Lorente et al. 2019). Most other notostylopids were of similar size.

As noted previously, remaining notoungulates are divided into toxodontians (toxodonts) and typotheres. Toxodonts were of medium to very large size, and many are known from postcranial elements or reasonably complete skeletons. Among the smaller toxodonts were so-called nothihippids, with estimated body masses of 12–16 kg (late Eocene *Puelia plicata*; Croft 2016) and ~20 kg (late Oligocene *Eurygenium pacegnum*; Shockey 1997). During the Paleogene, isotemnid and leontiniid toxodontians mainly filled larger notoungulate body-size niches. The body mass of the middle Eocene isotemnid *Thomashuxleya* has been estimated at 70–90 kg (Croft 2016, Carrillo & Asher 2017), and the late Oligocene leontiniid *Anayatherium fortis* probably had a body mass of 280–370 kg (Croft 2016). During the Neogene, particularly after the early Miocene, toxodontids were generally among the largest SANUs in South American ecosystems, exceeded in size only by astrapotheres (discussed later in this section). Late Pleistocene *Toxodon platensis* likely approached or exceeded 1,000 kg in mass (Fariña et al. 1998). The early Miocene clawed notoungulate *Homalotherium cunninghami* (discussed further in the section titled Postcranial Adaptations) weighed at least several hundred kilograms.

Typotheres notoungulates occupied small- to medium-sized herbivore niches in ancient South American mammal communities. The largest typotheres belonged to the family Mesotheriidae and generally had body masses from 30 to 75 kg (e.g., Croft et al. 2004), perhaps approaching

100 kg in Pleistocene *Mesotherium cristatum* (Bond 1999). Some hegetotheriid and interatheriid notoungulates were among the smaller typotheres, with body masses of 1–2 kg (e.g., Elissamburu 2004, Scarano et al. 2011). Early stem typotheres, such as the oldfieldthomasiid *Allalmeia atalensis* from the middle Eocene of northwest Argentina, were also small (~3 kg; Lorente et al. 2014). Oligocene and younger typotheres typically had body masses <10 kg (Croft & Anderson 2008, Reguero et al. 2010, Cassini et al. 2012).

Most Paleocene and Eocene litopterns, particularly those belonging to early-diverging groups, were small. For example, the protolipternid *Protolipterna ellipsodontoides* likely had a body mass of 500–1,500 g based on molar dimensions (Croft 2016). A notable exception in this regard were sparnotheriodontid litopterns (including *Sparnotheriodon* from Argentina and *Notiolofo*s from Antarctica), with estimated body masses of ~400 kg (Gelfo 2016). Proterotheriid litopterns (gracile litopterns) from the late Oligocene onward were of medium size, ranging from about 15 to 80 kg (Cassini et al. 2012, Croft 2016). Macraucheniid litopterns (robust litopterns) were generally larger than proterotheriids; most late Oligocene to late Miocene species were 80–120 kg (Cassini et al. 2012, McGrath et al. 2018), although a few were considerably smaller, such as middle Miocene *Llullataruca shockeyi* (35–55 kg; McGrath et al. 2018). Very large body size evolved in macraucheniids during the late Cenozoic (McGrath et al. 2019); Pleistocene *Macrauchenia patachonica* likely weighed 1,100 kg (Fariña et al. 1998), and *Xenorhinotherium babiense* from Brazil was at least as large, if not larger (McGrath et al. 2018). Middle Cenozoic adianthid litopterns (pygmy litopterns) were small; the body mass of early Miocene *Adiantus buccatus* was 7.4 kg based on p4-m2 length, and a lower leg bone of early Miocene *Adiantus godoyi* is about 90% the size of that of the proterotheriid *Thoatherium minusculum* (Scott 1910, Cifelli 1991), suggesting a body mass about 25% smaller (~10–20 kg).

Astrapotheres were among the largest SANUs, with many Oligocene and later species weighing between 1,000 and 3,000 kg (Kramarz & Bond 2011). These estimates are primarily based on craniodental measurements because astrapotheres are known from limited skeletal remains. An exception is a well-preserved skeleton of *Astrapotherium magnum* from the early Miocene of southern Argentina (discussed in the section titled Postcranial Adaptations). The specimen, once on display at the Field Museum in Chicago (see Riggs 1935, figure 39), has a head-body length of nearly 3 m, suggesting a body mass of 800–1,200 kg. Larger astrapotheres, such as late Oligocene *Parastrapotherium* spp. and middle Miocene *Granastrapotherium snorki*, likely weighed 2,000–3,000 kg (Kramarz & Bond 2011, Croft et al. 2019). Earlier-diverging astrapotheres, such as late Eocene *Trigonostylops wortmani*, were considerably smaller, around 20–40 kg (Croft 2016).

Pyrotheres were large to very large mammals. The geologically youngest and largest species was late Oligocene *Pyrotherium romeroi*, which may have weighed 3,000–3,500 kg based on dental measurements (Shockey & Anaya 2004). The teeth of other species are about 60% the size of those of *P. romeroi*, suggesting a body mass ~20% that of *P. romeroi* (600–750 kg). However, given the unusual, bilophodont dentition of pyrotheres, the accuracy of these tooth-based body mass estimates is uncertain. The skull length of *P. romeroi* is about 72 cm (Patterson 1977, figure 7), which suggests a head-body length of 2.9–3.6 m; using the head-body length equations of Damuth (1990) and Jerison (1971), a body mass of 1,800–2,700 kg may be more likely.

Like pyrotheres, most xenungulates were large mammals. *Carodnia vieirai* from Itaboraí, Brazil, is known from much of the postcranial skeleton; its head-body length was 1.5–2.0 m, and body mass estimates range from 200 to 650 kg (Croft 2016, Bergqvist & von Koenigswald 2017). Other *Carodnia* species were of similar size, but *Etayoa bacatensis* from Colombia, the smallest xenungulate, probably weighed only 5–10 kg (based on molar row length and geometric similarity with *Carodnia vieirai*).

**Loph:** a tooth structure used for shearing food that is formed by cusps that become confluent with wear

**Closed habitat:** a forest or other environment dominated by trees

**Cement:** a dental tissue on the external surface of a tooth that covers the root and sometimes extends onto the crown, increasing tooth's durability

**Open habitat:** an environment with relatively few trees

**Hypsodont:** having teeth with tall crowns; hypsodont premolars and molars are an evolutionary response to increased rates of tooth wear due to abrasive foods

**Carbon isotopes:** carbon atoms with different molecular weights preserved in teeth; variation in carbon isotope proportions can be used to assess whether an herbivore was feeding on grasses and in a forested or open habitat

**Microwear:** microscopic wear on a tooth surface (typically enamel); varies with diet in modern herbivores and can be used to determine diet in extinct mammals

## Diet

Bunodont teeth are nearly restricted to the litoptern lineage, with the caveat that the systematic positions of archaic ungulates or condylarths are not completely resolved. Bunodont dentitions are correlated with omnivorous diets in extant mammals (Janis 2007) and characterize Paleogene Kollpaniinae and Didolodontidae as well as Miocene megadolodine proterotheriid litopterns.

The simple crown pattern of Kollpaniinae is characterized by little molarization of their premolars. The small size of Kollpaniinae (see the section titled Body Mass, above) and the characteristic rounded cusps on their teeth likely constrained them to a frugivorous diet of non-fibrous plant matter (J.N. Gelfo, unpublished article). The more complex teeth of didolodontids (e.g., *Didolodus*; **Figure 5**) could be related to consuming insects, small animals, or even leaves. Didolodontids such as *Ernestokokenia*, in which additional cusps and shearing crests are less developed, may have consumed a higher proportion of fruits and seeds (J.N. Gelfo, unpublished article).

Megadolodine litopterns have teeth with relatively thick and strongly crenulated enamel and short yet robust roots, and their last two premolars show advanced molarization. Their omnivorous diet probably incorporated fruits with strong, thick rinds, and their teeth may have been useful for breaking the exoskeletons of crustaceans or even mollusks (Carlini et al. 2006; J.N. Gelfo, unpublished article). Other late Paleogene and Neogene litopterns were also brachyodont (low-crowned) but had postcanine teeth adapted for leaf- and stem-based browsing; the posterior premolars are molarized (increasing the area for food processing), and tooth surfaces have crescent-shaped lophs for shearing vegetation (**Figure 5**). Because browsing ungulates tend to feed in forested (closed) habitats, similar habits have been inferred for most litopterns (e.g., Cifelli & Guerrero 1997, Cassini et al. 2012). The narrow snouts of some litopterns have been cited as additional evidence for selective browsing (Cifelli 1991). Nevertheless, some Neogene litopterns had cement on their teeth, suggesting a more abrasive diet, perhaps in more open habitats (Bond et al. 2001, McGrath et al. 2018). This inference is supported by the presence of slightly more hypsodont teeth in late Miocene and younger litopterns (Bond 1999, Bond et al. 2011). Recent studies of stable carbon isotopes and enamel microwear in the geologically youngest proterotheriid, *Neolicaphrium recens*, concluded that it was a browser in open canopy forests (Corona et al. 2019, Morosi & Ubilla 2019). Stable carbon isotope data suggest that *Macrauchenia patachonica* was not a strict browser but rather had a diet that included both browse and grass (MacFadden & Shockey 1997).

The presence of extremely tall (hypsodont) teeth in notoungulates has long generated interest in the scientific community. It was this feature, in fact, that Richard Owen chose to highlight when he named *Toxodon*, which means bow-tooth; the ever-growing (hypsodont) upper molars of notoungulates such as *Toxodon* are so tall that they must curve toward the midline to fit in the upper jaw. Such teeth are not present in any living ungulate, but do occur in extant rodents, rabbits, and wombats (Metatheria: Vombatidae), and they evolved independently in four notoungulate families (Interatheriidae, Mesotheriidae, Hegetotheriidae, and Toxodontidae). In all of these groups, molar occlusal surfaces are simplified and composed primarily of dentine (**Figure 6**).

The parallel evolution of hypsodonty in several notoungulate families around the Eocene–Oligocene transition (**Figure 4**) has traditionally been interpreted as evidence for grazing in notoungulates (e.g., Patterson & Pascual 1968, Stebbins 1981) and the occurrence of grasslands some 15–20 million years earlier in South America than elsewhere (Flynn et al. 2003). However, exogenous abrasives ingested during feeding also contribute to hypsodonty (Janis 1988, Madden 2015), blurring the distinction between grazing in the strict sense (i.e., eating grass) and feeding on other types of plants in an open habitat. Paleobotanical evidence (Palazzesi & Barreda 2012, Strömberg et al. 2013, Dunn et al. 2015) combined with stable isotope data (Kohn et al. 2015) and the



# MAXILLA

## Henricosborniidae

# MANDIBLE



Posterior

Anterior



Posterior

Anterior

## Interatheriidae



## Mesotheriidae



## Hegetotheriidae



## Leontiniidae



## Notohippidae



## Toxodontidae



All scale bars = 1 cm

(Caption appears on following page)

**Figure 6** (Figure appears on preceding page)

Representative upper (left column) and lower (right column) teeth of notoungulates; anterior toward right in all images with tooth positions numbered sequentially from the front. Henricosborniidae: *Simpsonotus praecursor* (upper left I2–M3, shown as right; lower right i3–m3; MLP 73-VII-3-11). Interatheriidae: *Miocochilus anomopodus* (upper left I1–M3, shown as right; lower right i1–m3; UCMP 38091). Mesotheriidae: *Mesotherium cristatum* (upper right I1–M3; lower right i1–m3, shown as left; MACN 1113). Hegetotheriidae: *Hegetotherium mirabile* (upper right I1–M3, FMNH PM 13194) and *Paedotherium typicum* (lower right i1–m3, MLP 91-IV-5-66). Leontiniidae: *Ancylocoelus frequens* (upper right P2–M3, FMNH PM 13788; lower right i1–m3, FMNH PM 13494). Notohippidae: *Argyrobippus fraterculus* (upper right I1–M3, AMNH 29685; lower right p2–m3, AMNH 29731). Toxodontidae: *Pericotododon platignathus* (upper right P2–M3, UCMP 40199) and *Prototrigodon rothi* (lower right p1–m3, MLP 40-VIII-9-3). Abbreviations: AMNH, American Museum of Natural History, New York, USA; c/C, canine; FMNH, The Field Museum, Chicago, USA; i/I incisor; m/M, molar; MACN, Museo Argentina de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; p/P, premolar; UCMP, University of California Museum of Paleontology, Berkeley, USA.

ecological adaptations of the mammals themselves (Croft et al. 2008) suggest that the early evolution of hypsodonty in notoungulates occurred in open but relatively grass-free habitats (Su & Croft 2018).

From the late Oligocene onward, nearly all notoungulates had very hypsodont or hypselodont (ever-growing) premolars and molars (Figures 4, 6). However, not all of these species were feeding in open habitats despite their hypsodont teeth. MacFadden (2005) examined stable carbon isotope ratios from tooth enamel of large (~1,000 kg) Pleistocene toxodontids and found highly disparate values consistent with geographic variation in diet, ranging from browsing in closed forests (i.e., feeding on buds, twigs, and leafy vegetation) to grazing in open habitats. Similarly,  $\delta^{13}\text{C}$  values for Pliocene toxodontids (MacFadden et al. 1994, table 1) suggest they were open canopy browsers rather than grazers or mixed feeders, as might be assumed from their teeth. MacFadden (2005) concluded that late Pleistocene toxodontids were highly flexible in their feeding strategies and consumed the predominant local vegetation.

Townsend & Croft (2008) used microwear to infer the diets of three notoungulates from the early Miocene of southern Argentina: the toxodontids *Adinotherium* and *Nesodon* and the interatheriid *Protypotherium*. They found that all three were characterized by relatively fine microwear, more consistent with browsing than grazing, similar to that seen in modern leaf browsers such as moose (*Alces alces*), giraffe (*Giraffa camelopardalis*), and the black rhino (*Diceros bicornis*). Their interpretation contrasts markedly with that of Cassini et al. (2012), who investigated diet in the same three taxa (and other SANUs) via a multivariate analysis of craniodental morphology. Using a comparative data set of extant artiodactyls and perissodactyls, these authors concluded that *Protypotherium* and *Adinotherium* were likely grazers, *Nesodon* was probably a mixed feeder, and all three lived in open or mixed habitats. These results are not surprising given that habitat preference was inferred based on hypsodonty in addition to total jaw length, and diet was inferred assuming an open or mixed habitat (Cassini et al. 2012). Reconciling these interpretations will likely require applying additional taxon-independent methods of dietary reconstruction as well as a broader comparative data set for interpretations based on craniodental morphology, particularly for typotheres, which have many craniodental resemblances with hyraxes, rodents, and rabbits (Croft 2016, Ercoli et al. 2019).

Croft & Weinstein (2008) studied molar cusp shape (mesowear) in three typotheres notoungulates from the late Oligocene of Salla, Bolivia, and found that ground-level vegetation was apparently a major dietary component, with the proportion varying inversely with body mass: The mesotheriid, *Trachytherus alloxus*, had the most abrasive diet, similar to extant grazing ungulates; the interatheriid, *Federicoanaya sallaensis*, consumed more browse, similar to a modern mixed feeder; and the archaeohyracid, *Archaeohyrax suniensis*, had an intermediate diet. Thus, the diets of these notoungulates varied more than one might infer based on their similarly hypsodont teeth.

**Browser:** an animal that mainly feeds on leaves, stems, and buds of trees, shrubs, and relatively soft herbaceous plants

**Hypselodont:** having teeth that grow continuously from their base

**Grazer:** an animal that mainly feeds on grasses

**Mixed feeder:** an animal that feeds on a combination of grass and leaves, twigs, and buds of other plants

**Mesowear:** macroscopic wear on tooth cusps (or lophs); varies with diet in modern herbivores and can be used to determine diet in extinct mammals

No other studies have examined mesowear in SANUs, but the presence of high, pointed, browser-like cusps in other typothere notoungulates (e.g., *Hemihegetotherium trilobus*, Croft & Anaya 2006, figure 4; *Protypotherium endiadys*, Vera et al. 2017, figure 3F) casts doubt on the assumption that all were obligate open-habitat feeders. However, the presence of thick cement on the teeth of Oligocene and early Miocene notohippids (**Figure 6**) reinforces the presumption that these early hypsodont notoungulates were feeding on low, abrasive vegetation in open habitats (Bond 1986).

Gomes Rodriguez et al. (2017) recently documented that the four clades of notoungulates that evolved hypselodont dentitions also evolved accelerated eruption of permanent molars; in other words, all permanent molars erupted in these notoungulates before all of the premolars had been replaced. Such a co-occurrence of parallel changes has not been documented in any other group of mammals around the world; its causes and significance are uncertain and clearly warrant further investigation.

Astrapotheres have low-crowned teeth similar to those of modern rhinoceroses (**Figure 5**) and probably also chewed like them (Rensberger & Pfretzschner 1992). Given their large size, it is likely that astrapotheres fed almost exclusively on leaves and stems (as opposed to fruit), similar to modern browsing rhinoceroses. The skull morphology of Neogene astrapotheres suggests they had a proboscis (**Figure 1g**), and this organ was probably used in conjunction with the large tusks to strip leaves from branches (Johnson & Madden 1997). Kay & Madden (1997) suggested that middle Miocene astrapotheres and other megaherbivores may have had ecological roles similar to modern elephants in creating forest clearings by felling trees.

The teeth of many placental mammals show an enamel type characterized by layers of decussating enamel prisms, known as Hunter-Schreger bands (HSBs), whose arrangement likely varies with different mechanical requirements (e.g., resistance to crack propagation). In most cases, slightly undulating HSBs run horizontally around tooth crowns (von Koenigswald 1997), but in some groups (rhinocerotids, some extinct Asian tapiroids, and Dinocerata), they are vertically oriented, probably an adaptive response (rather than a phylogenetic signal). Among SANUs, vertically oriented HSBs are present in astrapotheres, congruent with browsing dietary habits, as well as in pyrotheres (Fortelius 1985) and sparnotheriodontid litopterns (Bond et al. 2006). Thus, these other taxa probably also fed on plant leaves with few abrasive elements rather than on grass, fruits, or seeds. As noted previously, pyrothere enamel is unusual in other aspects of its microstructure, but whether such features had special functional value is not known. On a gross level, pyrothere teeth functioned like those of modern bilophodont mammals, such as tapirs and kangaroos (Macropodidae), with a scissors-like action for shearing vegetation (von Koenigswald et al. 2015).

## Postcranial Adaptations

Nothing is known of postcranial adaptations of basal SANUs such as kollpaniids and didolodontids, and the only skeleton of a xenungulate presently known has yet to be described. A few postcranial elements of pyrotheres have been identified (all pertaining to late Oligocene *Pyrotherium*), but these provide little insight into the paleobiology of these mammals other than that they were flat-footed (plantigrade) and had columnar, graviportal limbs (Shockey & Anaya 2004). Given the relatively limited remains known for astrapotheres (discussed later in this section), the vast majority of studies of SANU locomotor adaptations have focused on notoungulates and litopterns.

Partial skeletons of Paleogene notoungulates are scarce, but the functional anatomy of a few middle Eocene notoungulates has been analyzed. A recent study of the basal notoungulate *Notostylops murinus* (Notostylopidae) from Patagonia (Lorente et al. 2019) concluded that it had digging tendencies (i.e., was semifossorial or fossorial), which is compatible with the hypothesis of Croft

**Cursorial:** having long limbs, often with small side digits, adapted for fast and/or efficient locomotion rather than maneuverability or power (as needed for climbing and digging)

& Anderson (2008) that this was the ancestral condition for notoungulates. In contrast, the stem typhothere *Allalmeia atalaensis* was likely digitigrade (i.e., standing with its heel off the ground) rather than plantigrade (the ancestral condition for mammals) and was terrestrial or perhaps even arboreal rather than fossorial (Lorente et al. 2014). Basal toxodonts (isotemnids) probably varied in their limb posture but were flat-footed (plantigrade) and not specialized for rapid locomotion (Shockey & Flynn 2007). The most significant modification to SANU postcranial morphology during the Cenozoic may have been the loss of the superior astragalus foramen, which presumably permitted greater range of extension at the ankle joint; this loss occurred in various lineages between the middle Eocene and late Oligocene, roughly concomitant with the evolution of hypsodont teeth in several SANU groups (Shockey & Flynn 2007).

Shockey et al. (2007) investigated the postcranial skeletons of mesotheriid notoungulates using both qualitative and quantitative approaches; the 30 extant taxa in their comparative data set included hyraxes, marsupials, carnivorans, large rodents, xenarthrans (armadillos and anteaters), and the armadillo (*Orycteropus afer*) in addition to artiodactyls and a perissodactyl (horse). They concluded that mesotheriids were most likely scratch diggers, an interpretation subsequently supported by the study of Fernández-Monescillo et al. (2018). Modern wombats have been proposed as the closest modern analogs for these notoungulates in terms of both skull and limb morphology (Croft 2016, Sosa & García López 2018) (**Figure 1f**). Croft & Anderson (2008) used an approach similar to that of Shockey et al. (2007) and concluded that the interatheriid notoungulate *Protyotherium* exhibited a generalized locomotor style tending toward cursoriality.

Clear cursorial specializations are present in a few Neogene notoungulates, but such modifications are not developed to the same degree as in most modern ungulates or in litopterns (discussed later in this section). The most extreme example of digit reduction in notoungulates is that of the interather *Miocochilius anomopodus* from the middle Miocene of Colombia, which supported its weight on only two digits (3 and 4), like modern artiodactyls. However, the limb proportions of *Miocochilius* are more similar to those of modern pigs and peccaries than deer and antelope, placing them among less cursorial modern ungulates (Stirton 1953). Some small late Cenozoic hegetotheriids such as *Paedotherium* spp. had limb proportions compatible with both cursorial and fossorial adaptations; their remains have been found in ancient burrows, and they probably resembled certain large rodents in their locomotor habits more than small artiodactyls (Elissamburu 2004).

Early-diverging toxodontians (notohippids) such as late Oligocene *Eurygenium pacegnum* have been interpreted as subcursorial generalists (Shockey & Anaya 2008), and their limbs terminated in four digits of similar size with hoof-like nails; the fifth digit was probably nonfunctional owing to its small size (Shockey 1997). A complete (albeit crushed) skeleton of the late Oligocene leontiniid *Scarrittia canquelsensis* has yet to be analyzed from a functional standpoint, but it indicates that the species had a longer neck than other toxodontians and may have had a slightly different foot posture in its forelimbs and hind limbs (Chaffee 1952). Early toxodontids such as early Miocene *Nesodon* and *Adinotherium* had robust limbs that were not specialized for cursorial locomotion (Cassini et al. 2012). The late Pleistocene toxodontid *Toxodon* had a passive stay mechanism for locking its knee joint in extension when standing, analogous to that of modern horses, and this feature evolved in the group by the late Miocene (Shockey 2001).

Arguably the most disparate SANU in terms of postcranial morphology was the large early Miocene toxodontian notoungulate *Homalodotherium cunninghami*; its limbs bore claws instead of hooves, similar to extinct chalicotheriid perissodactyls, and Coombs (1983) reconstructed it as a browser capable of standing on its hind legs. This interpretation fits with its low-crowned (brachydont) teeth and has been supported by a more recent analysis of its functional anatomy (Elissamburu 2010). Elissamburu (2010, 2012) estimated the mass of *Homalodotherium* at



~1,150 kg, but with a head-body length of just over 2 m (Riggs 1937, figure 55), a mass of 200–300 kg is more likely (see the section titled Body Mass, above). Cassini et al. (2012) estimated the mass of *Homalodotherium* at ~400 kg based on craniodental variables.

Litopterns were much more similar to modern ungulates in limb structure than were notoungulates and other SANUs (**Figure 1a,b**); middle to late Cenozoic litopterns had hinge-like limb joints, small lateral digits, and well-developed hooves, the latter indicating that they stood on the tips of their digits (i.e., they were fully unguligrade; Scott 1910). More basal litopterns, although not fully unguligrade, still had limbs specialized for running and perhaps jumping (Bastos & Bergqvist 2007). Such habits likely also characterized pygmy (adanthid) litopterns (Cifelli 1991). Litopterns for which relatively complete postcranial remains are known supported their weight on three digits (macraucheniiids) or only one (proterotheriids), and many cursorial adaptations were present in litopterns by the late Oligocene (Shockey 1999). These include a knee-locking mechanism like that of horses and some toxodontids (Shockey 2001) as well as very small side digits (Shockey 1999). The early Miocene proterotheriid *Thoatherium minusculum* is well known for having lateral digits proportionately smaller than those of modern horses (Scott 1937), yet even among Neogene litopterns, few species evolved distal limbs proportionately as long as those of modern cursorial artiodactyls and perissodactyls (Croft 2017). Whether this had any significant consequences in terms of performance is not known. Fariña et al. (2005) proposed that the transversely broad limb bones of the very large (~1,000 kg) Pleistocene litoptern *Macrauchenia patachonica* were an adaptation for swerving to escape predation. Similarly broad limbs do not characterize all litopterns, which probably used straight-line running as an escape strategy, perhaps in combination with swerving (McGrath & Wyss 2017).

A specimen of *Astrapotherium magnum* from the early Miocene of Santa Cruz, Argentina, is the most complete astrapothere skeleton known and displays a strange combination of features including a relatively long but robust neck, unusual limb proportions, a twisted tibial shaft, and gracile hindquarters compared to the rest of its body (Scott 1937, Weston et al. 2004, Croft & Guder 2014). Combined with large tusks and a proboscis, *Astrapotherium* and similar species were certainly among the most distinctive SANUs (**Figure 1g**). Riggs (1935, p. 176) indicated that remains of some astrapotheres are often found in riverine and lagoonal sedimentary layers and that their teeth were adapted for feeding on “low, moist-land plants.” He therefore reconstructed them as semiaquatic inhabitants of moist lowlands, an interpretation that generally has been followed in the scientific literature. Functional analyses of limb proportions (Cassini et al. 2012) and investigations of long bone histology (Houssaye et al. 2016) have not contradicted this interpretation but have not provided new evidence to support it.

## SYNTHESIS AND FUTURE DIRECTIONS

The development of powerful, relatively low-cost methods for scanning, studying, and reproducing specimens in three dimensions has profoundly affected the field of paleontology. These methods have been applied to studies of SANU morphology, paleobiology, and evolutionary relationships, but only in a limited fashion (e.g., Macrini et al. 2013, Dozo & Martínez 2016, Forasiepi et al. 2016). As machines and computational tools become more broadly accessible, new data sets will undoubtedly provide a wealth of new information about many aspects of SANU biology. However, this may be limited by the availability of such technologies in countries with limited financial resources; many important SANU specimens derive from economically developing countries and must remain in the country or institution in which they currently reside.

New technologies have allowed new data to be collected from century-old specimens, but the importance of continued fieldwork cannot be overemphasized. One priority must be discovering

new sites from little-sampled areas of the continent and poorly known time intervals that will help clarify SANU diversities and distributions. Another priority is continuing fieldwork at historically important sites. Many species (and even some families and orders) are known only from dental or craniodental remains; paleobiological and phylogenetic analyses would benefit immensely from more skulls and skeletons, and sites that have been producing similar specimens for generations are among the best places to find them.

As noted previously, we still lack a solid understanding of evolutionary relationships within and among the various groups of SANUs. This is partly due to limited material but mostly attributable to the absence of studies that have attempted to tackle such questions. Now that analyzing large phylogenetic data sets is commonplace, a concerted effort must be made to start building comprehensive character-taxon matrices of different data partitions (e.g., dentition, cranium, otic region, postcranium) that can be used to test the monophyly of Meridiungulata as well as clarify relationships with commonly recognized SANU groups.

Studies of SANU paleoecology have advanced substantially in recent years. Nevertheless, many questions remain. One area that merits further investigation is environmental tolerances and other factors that affected SANU diversity and biogeography. One striking pattern that presently lacks an explanation is the presence of astrapotheres and litopterns but not notoungulates in Antarctica. With the caveat that outcrops on Seymour (Marambio) Island have produced relatively few fossils, the absence of notoungulates is striking. Environmental tolerances or habitat preferences may be an adequate explanation, but timing of dispersals within southern South America could have been more important. The fossil record of both notoungulates and litopterns begins in the Paleocene (**Table 2**), but notoungulates are not recorded in Patagonia ( $\sim 45^{\circ}\text{S}$ ) until the early Eocene (Itaboraian; **Figure 4**). By contrast, litopterns were present in this area since at least the early Paleocene. If a shallow water barrier began to develop between South America and Antarctica during the early Eocene, or even an arid zone of land, it could have precluded notoungulates from dispersing to Antarctica by the time they arrived in southern South America.

Astrapotheres were less diverse than notoungulates and litopterns and maintained a relatively stable diversity of 3–4 genera from the late Oligocene through the middle Miocene (**Table 2**, **Figure 2**), but their geographic range constricted dramatically near the end of this interval, from essentially all of South America to only tropical latitudes (Bolivia and northward). Presumably this was related to climate and habitat changes following the middle Miocene Climatic Optimum (MMCO) (**Figure 4**) because a similar pattern is observed in certain other mammal groups (Croft et al. 2016), but a detailed understanding of the relationship between these changes and the ecological niches of astrapotheres is still lacking.

Unlike astrapotheres, litopterns and notoungulates were apparently unfazed by Miocene environmental changes, at least in terms of generic diversity; in both groups, diversity is essentially stable throughout the epoch (**Table 2**), especially when sampling differences among intervals are considered. Not evident in such numbers, however, are extinctions of four families during this interval, including adianthid litopterns and homalodotheriid, leontiniid, and interatheriid notoungulates (**Supplemental Tables 1–3**): a 45% reduction in SANU familial diversity. Like astrapotheres, leontiniids became restricted to low latitudes prior to their extinction, but this was not the case for the other families. Why these SANU families became extinct during this interval while others did not is an area ripe for future research. It might also help explain the dénouement of SANUs during the Pliocene and Pleistocene. Much faunal exchange took place between North and South America during this interval, commonly referred to as the Great American Biotic Interchange (GABI) (Woodburne 2010), and competition with (or predation by) North American invaders has been invoked to explain the extinction of the last SANUs (as well as many other groups of native South American mammals; Simpson 1950, Webb 1976). This view has

## Supplemental Material >

**Table 2** Number of South American native ungulate (SANU) genera recorded during the Cenozoic, based on data in Supplemental Tables 1–3

Ma <sup>a</sup>	Epoch	SALMA <sup>b</sup>	Taxonomic Group							SANU total
			Astrapotheria	Didolodontidae	Kollpaninae	Litopterna <sup>c</sup>	Notoungulata	Pyrotheria	Xenungulata	
<1	Pleistocene	Lujanian (Lu) <sup>d</sup>	0	0	0	4	2	0	0	6
2		Ensenadan (En)	0	0	0	5	2	0	0	7
3	Pliocene	Marplatan (Mp)	0	0	0	4	6	0	0	10
4		Chapadmalalan (Cp)	0	0	0	4	7	0	0	11
5		Montehermosan (Mo)	0	0	0	8	7	0	0	15
6–8	Miocene	Huayquerian (Hu)	0	0	0	13	17	0	0	30
9		Chasicosan (Cs)	0	0	0	4	12	0	0	16
10–13		Laventan (La) <sup>e</sup>	3	0	0	11	13	0	0	27
14–15		Colloncuran (Cc)	4	0	0	8	11	0	0	23
16–18		Santacrucian (Sa)	3	0	0	10	12	0	0	25
19		ND <sup>f</sup>	ND	ND	ND	ND	ND	ND	ND	ND
20–21		Colhuehuapian (Co)	4	0	0	8	9	0	0	21
22–23		ND	ND	ND	ND	ND	ND	ND	ND	ND
24	Oligocene	ND	ND	ND	ND	ND	ND	ND	ND	ND
25–31		Deseadan (De) <sup>g</sup>	4	0	0	9	33	1	0	47
32–33		Tinguirirican (Tg)	0	0	0	1	18	1	0	20
34–35	Eocene	ND	ND	ND	ND	ND	ND	ND	ND	ND
36–38		Mustersan (Mu)	2	3	0	4	16	3	0	28
39–42		Barrancan (Ba) <sup>h</sup>	2	4	1	5	30	0	0	39
43		ND	ND	ND	ND	ND	ND	ND	ND	ND
44–45		Vacan (Va) <sup>i</sup>	4	3	0	9	29	1	0	41
46		ND	ND	ND	ND	ND	ND	ND	ND	ND
47–48		Sapoan Fauna (SF)	3	4	0	3	13	0	0	21
49		ND	ND	ND	ND	ND	ND	ND	ND	ND
50–51		Riochican (Ri)	2	2	0	2	11	0	0	17
52–54		Itaboraian (It)	3	5	0	6	11	1	1	28
55–60	Paleocene	ND	ND	ND	ND	ND	ND	ND	ND	ND
61		<i>Carodnia</i> Zone (CZ)	0	0	0	1	0	0	3	3
62		ND	ND	ND	ND	ND	ND	ND	ND	ND
63		Peligran (Pe)	0	2	0	1	0	0	0	3
64		ND	ND	ND	ND	ND	ND	ND	ND	ND
65		Tiupampan (Tu)	0	0	5	0	1	0	0	6

<sup>a</sup>Ma, megannum (= million years ago).

<sup>b</sup>SALMA, South American Land Mammal Age. Allocated to one or more 1 million-year bins. Gaps represent intervals presently lacking a terrestrial mammal fossil record in South America. Two units (Sapoan Fauna and *Carodnia* Zone) have not formally been recognized as SALMAs but are included because they likely represent distinct temporal intervals. Abbreviations in parentheses are those used in Supplemental Tables 1 and 2.

<sup>c</sup>Includes families sometimes referred to Notopterna (Amilnedwarsiidae, Indaleciidae, Notonychopidae).

<sup>d</sup>Includes Bonaerian.

<sup>e</sup>Includes Mayoan.

<sup>f</sup>ND, no data (i.e., no sites of this age are currently known).

<sup>g</sup>Includes fauna of La Cantera.

<sup>h</sup>Younger part of Casamayoran SALMA.

<sup>i</sup>Older part of Casamayoran SALMA.

Supplemental Material >

moderated in recent years (e.g., Webb 1991, Simpson 1980), but the roles of predation and competition in the GABI have yet to be rigorously tested in terms of timing and niche occupation. Moreover, very large SANUs such as *Macrauchenia* (Litopterna) and *Toxodon* (Notoungulata) may simply have been casualties of the megafaunal extinction that swept through the Americas during the late Quaternary. The causes of this phenomenon continue to be debated, but humans were probably an important causal factor (Cione et al. 2003, Barnosky & Lindsey 2010).

The native peoples of South America surely viewed SANUs such as *Toxodon* and *Macrauchenia* as typical members of the landscape, no more peculiar than deer, peccaries, and horses are to the inhabitants of present-day South America. Although we can rightly lament that we barely missed these ancient inhabitants (at least in terms of geological time), one cannot help but wonder: If these distinctive mammals had not gone extinct, would they have inspired such wonder in the mind of Darwin? And if not, how might that have impacted his ideas about evolution and natural selection? The extinction of the SANUs was a significant loss for Neotropical biodiversity, but perhaps it was fortuitous for evolutionary biology. Paleontologists have resurrected many aspects of SANU evolution and ecology in the decades since pioneers such as Owen, Ameghino, and Roth struggled to make sense of these peculiar mammals. But by contributing to the development of the most far-reaching theory in biology, we would argue that SANUs are still with us today.

## SUMMARY POINTS

1. South American native ungulates (SANUs) include five major and several minor groups of extinct plant-eating mammals whose fossil record is almost exclusively confined to South America.
2. Some SANUs seem to be most closely related to horses and rhinos (perissodactyls) among extant mammals, but it is not known whether all SANUs constitute a monophyletic group (Meridiungulata).
3. Notoungulates, the most diverse group of SANUs, included several lineages that independently evolved ever-growing molars but likely varied in their diets.
4. Litopterns evolved cursorial limb specializations early in their evolutionary history but seem to have mostly inhabited forested or partly forested environments.
5. Geologically younger astrapotheres were very large, tusked, proboscis-bearing mammals that became restricted to the northern half of South America prior to their late Miocene extinction.
6. Pyrotheres and xenungulates, relatively poorly known Paleogene SANUs, both evolved bilophodont teeth, yet whether they are closely related to one another remains to be determined.
7. Litopterns and astrapotheres are among the few terrestrial placental mammals that dispersed to Antarctica in the early Eocene.
8. SANU generic diversity was high from the early Eocene through the late Miocene (~20–40 genera), but familial diversity gradually declined after the early Miocene; five families survived into the Pliocene, and the last SANUs went extinct in the late Quaternary megafaunal extinction.



## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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## Errata

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